# RIVERSLEIGH BIRDS AS PALAEOENVIRONMENTAL INDICATORS

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Fossilised birds from Riversleigh are used to make a palaeoenvironmental reconstruction. Difficulties that hamper this attempt are discussed. From the early to early late Miocene deposits, a range of taxa demonstrate aquatic situations; four others are indicative or at least suggestive of rainforest; one hints at at least some open spaces; and six are ambiguous because of insufficient morphological variation between taxa with different ecological preferences or insufficiently known palaeobiology. The only species thus far identified from Pliocene Rackham's Roost Site points to conditions similar to those at Riversleigh today. □
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Modern birds are excellent habitat indicators. Potentially, the Tertiary avifauna of Riversleigh could serve a valuable role in interpreting the palaeoenvironment. Numerous bird remains have been recovered, but few have been studied (Rich, 1979; Boles,1991, 1993a, b, c, 1995, 1997a, b).

Based primarily on the diverse mammal remains, Archer et al. (1989) interpreted the vegetation of Riversleigh during the early to early late Miocene as 'dense, species-rich gallery rainforests probably similar to those that persist today in mid montane New Guinea'. Archer et al. (1994) concluded that the surrounding Pliocene habitat was 'a dry sclerophyll forest or woodland with a grassy understorey, probably not too unlike the environment that dominates Riversleigh today'. This paper reviews available information about Riversleigh birds as it might contribute to interpretations of Tertiary environments.

Material (Table 1) is lodged in the Queensland Museum (QM) and Australian Museum (AM). The geology and geography of the Riversleigh deposits are available elsewhere (Archer et al., 1989, 1994, 1995; Megirian, 1992).

## INTERPRETATION OF HABITATS: BASIC TENETS

One of the most striking features of the Riversleigh avifauna is the large proportion of small terrestrial forms compared to other middle Tertiary sites in Australia, which are largely dominated by waterbirds and larger, flightless forms, both of which are also present at Riversleigh. Among modern Australian terrestrial (non-aquatic) birds, the prevailing pattern is considered to be that the more primitive (least specialised) members of lineages are found in montane and subtropical rainforest and contiguous wet forests, whereas the more derived taxa occur in open habitats. Schodde & Faith (1991) considered that 'rainforest-inhabiting members, particularly in montane New Guinea and subtropical Australia, represent ancestral forms from which those in sclerophyll vegetation have been derived'. These ancestral components have been recognised as the Tumbunan fauna (Schodde & Calaby, 1972; Schodde, 1982; Schodde & Faith, 1991). The Tumbunan avifauna is now largely centred on 'a *Nothofagus*-myrtle-podocarp-dominated forest of the type once widespread across Australia through the mid Tertiary' (Schodde, 1982), although some elements of this fauna now extend well beyond this habitat. Although the Tumbunan-type habitat is now mostly restricted to higher elevations, a distribution that is relictual, it was once more widespread through lower altitudes. Schodde & Faith (1991) suggested that 'the subtropical Tumbunan avifaunas now present in montane New Guinea were widespread in Australia' in the mid-Tertiary. Thus the habitat of Riversleigh during the Miocene was probably similar to that retained in these present Tumbunan refuges.

This apparent relationship between level of specialisation and habitat has been adopted as a basis for palaeoenvironmental interpretation. A fossil taxon is tentatively considered a likely rainforest inhabitant if it is primitive in its lineage. It may also be considered to occur in rainforest if its affinities are to a group that is today confined to rainforest. If all living species occur in a certain habitat then that habitat is considered to most likely for the fossil form.

mated hindlimb proportions of *E. gidju* with those of Recent *Dromaius* and *Casuarius*. The tibiotarsus and tarsometatarsus of *E. gidju* were relalower leg permits these birds to capture prey from hollows and recesses inaccessible to other predatory birds. Modern species occur in a range of

There seems little problem with freshwater aquatic birds. Within a family, there may be some variation in the type of aquatic habitats preferred, although the range of differences is substantial in only a few instances. Modern habitat preferences are used as an indication of the fossils' palaeohabitats, unless otherwise indicated.

Unless there is some outstanding morphological feature that signals a major shift in its biology, a fossil bird is considered to have similar ecological characteristics as its modern counterparts. Similarities in morphology between fossil and living forms are interpreted to share similar functions, unless there is evidence to the contrary.

## SYSTEMATIC LIST

### Dromornithidae

This extinct family comprises 8 species in 5 genera (Rich, 1979). These were large, flightless birds with major, 'ratite'-grade modifications to an entirely terrestrial lifestyle. The extent of these masks any relationships to other known orders of birds, although this family is no longer considered closely allied to living ratites (Olson, 1985).

*Barawertornis tedfordi* and *Bullockornis planei* occur at Riversleigh as conspicuous faunal elements at some sites because of their abundance and size. Despite this, they are limited palaeoenvironment indicators because little is understood of their biology. The 2 monotypic Riversleigh genera are among the least known.

At Riversleigh, the 2 species occur together, often, but not always, with other large animals (e.g., D-Site). At several sites they occur with aquatic animals such as lungfish, turtles and crocodiles. Whether this is an indication of a waterside association or a taphonomic artefact is not known. Nothing in the foot structure is obviously modified for entering water, nor has there been previous suggestion of an aquatic association.

Relative proportions of the hindlimb bones can be a useful indication of locomotory mode. In few dromornithid species, however, are complete specimens known for all major leg elements, and these rarely represent the same individual. Reconstructions must necessarily be based on the better known forms, particularly *Genyornis newtoni*. Estimates of leg proportions are based on measurements given by Rich (1979). The hindlimb proportions of most dromornithids are very different from those of *Casuarius* or *Dromaius*, with only *Ilbandornis lawsoni* having proportions approaching those of living emus; Rich (1980) and Vickers-Rich (1991) considered this the most cursorial species. Where known, the tarsometatarsus of other species is short relative to the other long bones, more like the moas .

The moas (Worthy, 1991) provide some suggestions about aspects of dromornithids' lifestyle. Most moas were forest dwellers, almost exclusively herbivorous. None seemed adapted to cursorial locomotion. Moa remains are often recovered in large numbers, indicating that these were gregarious birds. Many Australian dromornithid sites yield large numbers of specimens, indicating aggregations. Such a concentration of animal biomass is analogous to moas and suggests that dromornithids were herbivorous (Vickers-Rich, 1991).

The dromornithid bill was much heavier and deeper than the moas' (Olson, 1985, fig. 3; Vickers-Rich, 1991, pl. 4). The skull was larger and more robust, with scars indicating broad attachments for the jaw muscles (P. Vickers-Rich pers. comm.). Regardless of what dromornithids ate, they were equipped to handle more substantial food items than were moas. Their bills are not hooked or otherwise suggestive of a predatator.

Unlike moas, no remains of dromornithid food have been found. Large accumulations of dromornithid gastroliths (gizzard stones) occur at Riversleigh (Archer et al., 1994:79) and other sites (Stirling & Zeitz,1900; Vickers-Rich, 1991).

By the late Miocene, both graviportal and cursorial species lived in northern Australia. This was taken to indicate both forest and open country by Rich & Baird (1986), who did not consider dromornithids to have been particularly successful in invading grasslands. The Riversleigh fossil material does not show cursorial modifications. It can be tentatively concluded that *Barawertornis* and *Bullockornis* were forest dwellers.

### Casuariidae - emus and cassowaries

*Emuarius* Boles, 1991 occurs at Riversleigh. Living emus and cassowaries *Casuarius* are quite different in their habitat preferences and locomotory styles. The latter is reflected in the hindlimb, suggesting potential for inferring palaeohabitat from a comparison of *E. gidju* with living forms.

Patterson & Rich (1989) found that the phalanges of *E. gidju* were between those of *Dromaius novaehollandiae* and *Casuarius* in morphology, although more similar to the former in relative lengths and in degree of dorsoplanar compression. The fossil form *D. ocypus* Miller, 1963 had a tarsometatarsus that is markedly shorter relative to its width than that of *D. novaehollandiae*, but longer than *Casuarius*. Vickers-Rich (1991) in-

TABLE 1. Bird families in Riversleigh Tertiary deposits and sites from which these have been recovered. A=Dromornithidae; B=Casuariidae; C=Phalacrocoracidae; D=Ciconiidae; E=Anatidae; F=Accipitridae; G= Rallidae; H=Cacatuidae; I=Psittacidae; J=Apodidae; K=Halcyonidae; L= Passeriformes ([1] =Menuridae; [2] =Oriolidae; [3] = Orthonychidae).

| SITE | A | B | C | D | E | F | G | H | I | I | K | F |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| SYSTEM A | | | | | | | | | | | | |
| D-Site | X | | | | | | | | | | | |
| D-SITE EQUIVALENT | | | | | | | | | | | | |
| Sticky Beak | X | | | | | X | | | | | | |
| SYSTEM A OR B | | | | | | | | | | | | |
| White Hunter | | X | | X | X | X | X | | | | | X |
| SYSTEM B | | | | | | | | | | | | |
| Camel Sputum | X | X | X | | | | X | | | X | | X |
| Helicopter | X | | | | | | | | | | | |
| Outasite | | | | | | | | | | X | | X |
| Panorama | | | | | | | | | | | | X |
| RSO | X | | | | | | | X | | X | | X |
| Upper | X | X | | | | | | | | | | X[1] |
| Wayne's Wok | X | | X | | | | | | | | | X |
| Wayne's Wok II | | | | | | | | | | | | X |
| Neville's Garden | X | | | | | | | | | | | X[2] |
| SYSTEM ?B | | | | | | | | | | | | |
| Bitesantennary | | | | X | | | | | | | | |
| Dirks Towers | | X | | | | | | | | | | X |
| Microsite | | | | | | | | | | | | X |
| SYSTEM C | | | | | | | | | | | | |
| Archie's Absence | | | | | | | | | | | | X |
| Henk's Hollow | | | | | | | | | | | | X |
| Gag | | X | | | | | | | | | | X |
| Gotham | | | | | | | | | | | | X |
| Jim's Carousel | | | | | | | | | | | | X |
| Last Minute | | | | | | | | | | | X | X[3] |
| Ringtail | | | | | | X | | X | | | | X |
| Two Trees | | | | | | | | | | | | X |
| PLIOCENE | | | | | | | | | | | | |
| Rackham's Roost | | | | | | | | | X | | | X |

terpreted this to mean that *D. ocypus* was less cursorial than *D. novaehollandiae*. *Emuarius gidju* approaches *D. novaehollandiae* in tarsometatarsal length:width ratio more closely than does *D. ocypus* (Boles, this volume a).

Increased cursoriality in the Casuariidae is characterised by an increase in the lengths of the tibiotarsus and tarsometatarsus relative to the femur. Boles (this volume a) compared the estimated hindlimb proportions of *E. gidju* with those of Recent *Dromaius* and *Casuarius*. The tibiotarsus and tarsometatarsus of *E. gidju* were relatively longer than in any other casuariid, except *D. novaehollandiae*. The structure of the phalanges, relative width of the tarsometatarsus and proportions of the hindlimb suggest that *E. gidju* was more cursorial than *Casuarius* and may have approached the ability exhibited by *D. novaehollandiae*. *E. gidju* may have had habitat preferences resembling those of *D. novaehollandiae*, i.e., largely open country, although some rainforest types could possibly offer a sufficiently open understorey.

Phalacrocoracidae - cormorants

A distal carpometacarpal fragment comes from a large cormorant. Beyond signaling a lacustrine situation, it is uninformative.

Ciconiidae - storks

Stork remains comprise 1 proximal and 2 distal tarsometatarsal fragments, 1 quadrate and a partial skull. The tarsometarsi do not belong to *Ephipphiorhynchus*, the only living genus in Australia, and are probably referable to *Ciconia*, a genus now found in Eurasia, South America and Africa. All living storks have associations with shallow, slow moving water, although they are not restricted to aquatic habitats; they do not enter heavily forested areas. All eat small animals, including vertebrates, and some (*Leptoptilos*) consume carrion.

Anatidae - waterfowl

Several specimens have been allocated to this family but no further determination has been made. Subgroups of living waterfowl have circumscribed habitat preferences. The Riversleigh specimens indicate aquatic, probably lacustrine, situations.

Accipitridae - diurnal birds of prey

*Pengana robertbolesi*, a large bird of prey, with hyperflexible tarsal joint (Boles, 1993a) is convergent with the living *Polyboroides* (Africa) and *Geranospiza* (South America). Mobility of the lower leg permits these birds to capture prey from hollows and recesses inaccessible to other predatory birds. Modern species occur in a range of

habitats and do not permit any meaningful extrapolation to Riversleigh. A femoral fragment of this family is of comparable size to *Pengana*, but can be referred only tentatively to this taxon.

Rallidae - rails

There is much rail material, representing most forelimb and hindlimb elements, from several sites, but most abundantly at White Hunter site, possibly from a single individual. All specimens represent a medium-sized rail about the size of living *Gallinula tenebrosa*. From the shape of the carpometacarpus and the relative sizes of the wing and leg elements, it appears to have been flightless. This rail is probably related to the native-hens *Tribonyx*, now usually merged as a subgenus of *Gallinula*. The native-hens comprise two living endemic Australian species, one of which is flightless, and a flightless Pleistocene species endemic to New Zealand. Although largely remaining in the vicinity of water, both Australian species freely enter adjacent open country. The flightless Tasmanian *mortierii* enters cultivated paddocks, and mainland *ventralis* may move some distance from water in semiarid and arid regions. Species of *Gallinula* are gregarious, which is consistent with the number of fossils found at some sites. The Riversleigh rail indicates the proximity of wetlands, but little else about the local environment.

Cacatuidae - cockatoos

A rostrum has been referred to the modern white cockatoos, *Cacatua* (Boles, 1993b). Within Australia, these species occur from rainforest fringes through open forest and woodland to open arid country. The Riversleigh bird is considered to have been similar to the group of white cockatoos with small bills and rounded, uncoloured crests, such as the corellas. These species exhibit a considerable range of habitat preferences, from central Australian arid zone (*C. pastinator*) to rainforests on some islands e.g., Solomon Islands (*C. ducorpsii*). This range of habitats occupied by modern species renders the Riversleigh specimen of little value in palaeohabitat reconstruction.

Psittacidae - parrots

Two carpometacarpi and a tarsometatarsus from Rackham's Roost come from the living Budgerigar *Melopsittacus undulatus*. This is a good indication that the Pliocene habitat at Riversleigh was open and lightly timbered. Today this species occurs in the arid, semi-arid and subhumid zones, including Riversleigh, but never far from water.

Apodidae - swifts

Humeri, a coracoid and tarsometatarsus of a medium-sized swift are close to a large species of swiftlet *Collocalia*, the only genus that breeds in Australia at present. These species nest in caves, but, despite the number of apparent Riversleigh deposits originating from cave floors, surprisingly few remains have been found at Riversleigh thus far. One of the bones is that of a young bird, strong indication that at least some level of local breeding was taking place. Swifts are not good environmental indicators, because they are aerial feeders, capturing flying insects above the habitat canopy, irrespective of what that habitat may be.

Halcyonidae - forest kingfishers

The single specimen available is assigned to the Halcyonidae, possibly close to *Todiramphus* (Boles, 1997b) and similar to more primitive living halcyonids (*Tanysiptera*, *Melidora*, *Syma*), which are rainforest inhabitants (Fry, 1980a,b). The Riversleigh fossil resembles what would be predicted for an early member of the *Todiramphus* lineage. Australian *Todiramphus* occur outside rainforest, but species of the genus live in rainforests in other parts of Australasia.

Passeriformes - songbirds

These birds are good habitat indicators at specific or generic level. Songbirds are known from about 100 specimens from at least 20 sites (Boles, 1995); however, only 3 specimens thus far provide useful habitat indications. *Orthonyx kaldowinyeri*, of which a femur has been reported (Boles, 1993c), belongs to a genus with the 2 living species confined to rainforest of the east coast and New Guinea, occasionally entering dense bordering vegetation (e.g., *Lantana*). Green Waterhole Cave, SE South Australia, the site for *O. hypsilophus*, never had rainforest, but there is evidence for a thick cover of *Leptospermum* (Baird, 1985), which would probably have provided adequate cover.

The lyrebird *Menura tyawanoides* is represented by a carpometacarpus (Boles, 1995). The two living species occupy rainforest and, in the case of *M. novaehollandiae*, contiguous forest. The habitat preferences of the Riversleigh species of *Orthonyx* and *Menura* are assumed to be similar to those of their modern congeners.

A large lower mandible from Neville's Garden Site (unpubl. data) is from the Oriolidae which

includes the frugivorous forest birds *Oriolus* and *Sphecotheres viridis*; many occur in closed forest. The fossil suggests rainforest, but is not diagnostic.

## TAPHONOMY

None of the aquatic or semi-aquatic species, except the *Gallinula*-type rail, show any evidence of unusual causes of death or accumulating agents. The rails occur in greater numbers at a handful of sites, possibly due to a gregarious habit rather than taphonomy. Dromornithid remains being very common at some sites may also be a result of gregariousness or their corpses could have been accumulated during flooding. They are often found with large aquatic taxa (e.g., lungfish, turtles, crocodiles), and these may represent thanatocoenoses. Most other terrestrial species are too infrequent to provide any clues, but may be best considered chance survival of the remains of animals that died for a variety of reasons.

Exceptions are the small terrestrial forms, particularly passerines, which appear to have been killed by ghost bats *(Macroderma)*. The living *M. gigas* is a predator of small vertebrates, which it captures from the ground or perch. Prey are eaten in the roost caves by chewing through the pectoral region, manifested in the skeleton as extreme damage to the sternum (Boles unpubl. data); distal wings and legs are discarded. This is consistent with the elements that predominate at former *Macroderma*-accumulated sites at Riversleigh (carpometacarpus, tibiotarsus, tarsometatarsus). Unlike northern Australia today, where only a single species exists, Riversleigh is known to have supported many species of ghost bats during the Tertiary (Hand in press). Several sites have been identified as the remnants of *Macroderma* roost caves, such as the Miocene Gotham Site and the Pliocene Rackham's Roost Site.

## PROBLEMS IN INTERPRETATION

There are several reasons why the Riversleigh birds do not offer the same depth of environmental data as living forms. Many specimens are yet to be studied. Ordinal level identification (Table 1) is frequently not fine enough for meaningful habitat inferences, especially for terrestrial species. There may be insufficient morphological differences between related forms occupying different habitats. Much of the biology of extinct groups remain unknown. Basic assumptions could be wrong; primary ones employed here are that fossil birds had similar ecological characteristics to living counterparts and within a lineage more primitive species occur in rainforests, more derived ones in more open habitats.

## PALAEOENVIRONMENT

The birds show that both aquatic and terrestrial habitats were prominent through the early to mid Miocene at Riversleigh. Because of the broad spectrum of wetland situations in which they occur, the cormorant, ducks and rail do not provide any clues to the detailed nature of these systems. Based on modern habitat preferences, the stork indicates shallow, slow moving, lacustrine situations somewhere in the area.

Several of the better taxonomically resolved specimens are consistent with a closed forest. The passerines *Orthonyx* and *Menura* belong to families which are today almost exclusively restricted to rainforest. Living halcyonid king fishers occur through most Australian habitats; the Riversleigh form, however, is suggestive of more primitive, rainforest-inhabiting taxa.

Possible support for a more open habitat in some places comes from *Emuarius*. Its hindlimb proportions are thought to resemble those of *Dromaius novaehollandiae*, a highly cursorial animal. If the assumption can be made that the similarities in morphological proportions of the hindlimbs reflect similarities in function, this implies an advanced level of cursoriality in *Emuarius* as well.

The Pliocene environment of Riversleigh, based on Rackham's Roost site, was quite different from the Miocene. The Pliocene fossils are all small forms, mostly passerine but including a small extant parrot, *Melopsittacus undulatus*. This species is widespread, in arid and semiarid woodlands and scrublands, including the Riversleigh area. It requires proximity of water. Thus it suggests that Riversleigh in the Pliocene was probably very much like it is today.

The Riversleigh early to mid Miocene environment probably included shallow water at a number of different sites, with some surrounding rainforest and some more open forrests.

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